PREDATORY BEHAVIOR AND PREY OF *DIOGMITES MISSOURIENSIS* BROMLEY IN ARKANSAS (DIPTERA: ASILIDAE)¹

AUBREY G. SCARBROUGH

Associate Professor, Department of Biology, Institute of Animal Behavior, Towson State University, Baltimore, Maryland 21204.

Abstract.—Diogmites missouriensis Bromley was concentrated in areas of the study site where prey and prey activities were maximized. The asilids perched on low vegetation and surveyed the immediate area for prey using characteristic head and body movements. Foraging flights were usually short and unsuccessful. Prey were usually captured in flight and carried to perches where they were immobilized. Feeding times and number of prey manipulations were correlated with prey characteristics. Hymenoptera and Diptera were most frequently taken as prey. Over 90% of the prey were 14 mm or less in length. Females were larger, took larger prey, and had a wider range of prey than males. Males captured primarily Hymenoptera, especially halictid bees.

Diogmites missouriensis Bromley is a medium sized (17–26 mm) pale reddish-gold robber fly. It is recognized by three black mesonotal stripes of which the central one is divided longitudinally for its entire length and extends to, or almost to, the pronotum (Bromley, 1951). Diogmites missouriensis is similar to D. salutens Bromley, but differs in having darker mesonotal markings and lacking the blackish bands on the dorsum of the abdomen (Artigas, 1966). The species has been found in weedy areas, cotton fields, and vegetable gardens (Bromley, 1951; Scarbrough, 1972). Diogmites missouriensis was described by Bromley in 1951 but was mentioned in an earlier publication (Bromley, 1950). A recent morphological description of the species and a key to the genus Diogmites in the eastern United States are given by Artigas (1966).

STUDY SITE AND METHODS

Diogmites missouriensis was studied at two locations on the outskirts of Jonesboro, Craighead Co., Arkansas. General observations on predation

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Fig. 1. Percent feeding and total numbers of *Diogmites missouriensis* during a 5-day hourly census between 28 July and 8 August 1978.

were taken in weedy fields along Christian Creek in southwestern Jonesboro during the summers of 1963 and 1964. More extensive observations on predation were taken from July 26 to August 8, 1978, in a 22-acre plot, located on the south-side of Jonesboro. The plot was once part of a large cultivated field which has been subdivided recently into small plots and zoned for commercial development. It is bordered by commercial roads (Jonesboro Bypass, Caraway, and Young Roads) and other underdeveloped commercial plots. The portion of the plot in which most observations were taken was dominated by several herbaceous plants, common to old field succession. Most plants ranged from 30–90 cm in height, forming a dense vegetative mat. Dominant plants, *Digitaria* sp., *Polygonum* sp., *Allium vineale* L., *Ambrosia bidentata* Michx., *Campsis radicans* (L.) Seem., and *Xanthium spinosum* L. formed small isolated clumps. About one-fourth of the 22-acre plot contained open woods in which *Quercus* spp. were abundant.

This study was conducted under bright sunlit conditions and temperatures ranging from 25 to 39°C. All observations began at 0700 hrs and continued until 1900 hrs. During 1978, a census was taken of individuals every hour during a 5-day period by slowly walking along a designated route of about 600 m through the study plot. All asilids observed and their behaviors were recorded. Prey captured by *D. missouriensis* were recorded and captured,

whenever possible, by netting individuals with prey. Most prey captured were pinned, later identified, and then measured from the frons to the tip of abdomen for body length. A total of 50 specimens of *D. missouriensis* was collected, sexed, and measured. Observations were also made on predatory behavior on occasions other than during the census.

PREDATORY BEHAVIOR

Diogmites missouriensis occurs among herbaceous vegetation in open, sandy, well-drained fields during July and August in northeastern Arkansas (Scarbrough, 1972). The asilids were abundant in the study area (Fig. 1), with 20 or more flies during most census periods. Like several bee-and-wasp killing asilids (Linsley, 1960, 1972), D. missouriensis was concentrated in areas of the study site where prey and prey activities were maximized around flowering plants of Polygonum sp. and Stellaria sp. The asilids apparently conducted all behaviors in open areas of the study site and were not seen to move into adjacent wooded areas.

Diogmites missouriensis usually perched in a foraging position on low vegetation (N = 2060 observations, range 1–105 cm in height; 92% below 60 cm) in full view of its surroundings. Upon landing, the asilids oriented their bodies with their heads facing the sun or with their bodies positioned at a right angle to the sun's rays. This behavior was followed by rapid vertical and lateral head movements. Intermittently between head movements, the asilids moved their bodies slightly to the right or left of their original position. Head movements followed each body shift. In effect, the asilids shifted their bodies 360°, and surveyed the immediate area around a perch for prey. If movements of a potential prey were detected, the predator directed its head toward the prey and shifted its body weight forward into an attack posture. Diogmites angustipennis Loew (Lavigne and Holland, 1969) displays similar head and body movements on its foraging perch. These behaviors apparently enhance the asilids' ability to detect prev movements within the immediate area surrounding a perch and, consequently, reduce the need for more frequent flights.

Normal flight patterns were associated with foraging, disturbance, and searching behaviors. Most flights were short ($\bar{x} = 210$ cm, range 7–1615, N = 480) and a few cm (about 2–5) above the vegetation. Disturbed flies varied greatly although they usually flew longer distances ($\bar{x} = 782$ cm, N = 30) between perches and higher (>6 cm) above the vegetation. In search of females with which to mate, males flew slowly with legs outstretched in a manner similar to that described for *D. angustipennis* (Lavigne and Holland, 1969). These flights were erratic, often combined with hovers, and followed the contours of the vegetation. Distances between perches were variable but a male frequently traveled 20 or 30 m before perching.

Observations of individual flies revealed that the frequency of changing

perches was variable, depending upon the time of day and prey availability. Although prey densities were not determined, it can be assumed that feeding rates are directly related to prey availability. In early afternoon (1200–1500 hrs) when feeding rates were high, *D. missouriensis* changed perches frequently (N = 20 flies, $\bar{x} = 18/hr/fly$, range 9–29/hr). In late afternoon (1630– 1830 hrs) when feeding rates were low, they changed perches less frequently (N = 20 flies, $\bar{x} = 6/hr/fly$, range 0–12/hr; *P* < .05). Flies rarely flew after 1730 hrs and usually crawled below a leaf or into a plant's interior where they remained overnight.

Observation of 12 different flies (1200–1300 hrs) revealed that foraging behaviors consisted of short darting flights (N = 156, $\bar{x} = 10.2$ cm, range 3.0–47.0). General attack strategies of *D. missouriensis* consisted of direct dart flights from perches or indirect flights in which the asilid flew slowly from a perch, hovered, and then darted toward the prey. In both strategies *D. missouriensis* sometimes approached prey by short flights, landing on a series of perches.

The above observations also revealed that *D. missouriensis* foraged frequently (N = 156, $\bar{x} = 13/hr/fly$) but seldom captured a prey. Only seven prey were captured during these observation periods. The asilid behaved similarly in late afternoon (1630–1730 hrs) with only two successful flights (N = 10 flies, 21 flights, $\bar{x} = 2.1/hr/fly$) but foraged less frequently. Combined data during the study supported these results with 99 or 12% (N = 832) of the flights successful.

Foraging success was directly related to the potential prey's association with vegetation and the inability of *D. missouriensis* to detect and to navigate around vegetation during an attack. Prey were invariably crawling on or flying near vegetation. When the asilid foraged, it (N = 35, 22% of 156 flights) frequently flew into the vegetation, missing its prey. In most instances (78%), it landed as soon as the prey disappeared among vegetation.

Like *D. angustipennis* (Lavigne and Holland, 1969), *D. missouriensis* captured over 96% of its prey (N = 197) in flight. The remaining 4% were captured crawling on vegetation. On each occasion, the asilid grasped the prey with one fore tarsus while supporting itself with the remaining tarsi. It subsequently grasped the prey with the remaining tarsi before flying to a new perch. *Diogmites misellus* Loew (Bromley, 1946) and *D. angustipennis* (Lavigne and Holland, 1969) sometimes capture crawling prey.

Upon capture, live prey were carried in flight suspended below the asilid's body with all tarsi to a perch. There, the asilids perched below a leaf or stem, suspended by their right or left fore leg. Live prey were then manipulated with the remaining tarsi into a position where the hypopharynx was inserted, and they were subsequently immobilized. Prey were often removed from the asilid's hypopharynx during feeding and manipulated with the free tarsi, and the hypopharynx was inserted at a new location.

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The time spent feeding and the number of manipulations were highly variable and were related to prey size. Small halictid bees (N = 24, $\bar{x} = 5.5$ mm, range 4.5–7.5) were fed upon for an average of 15.2 min (N = 20 prey, range 7–19 min) and manipulated three times (N = 20 prey, range 1–5). In contrast, large asilid prey (N = 25, $\bar{x} = 17.9$ mm, range 15.0–21.3) were fed upon for 48.2 min (N = 11, range 40–62 min) and manipulated six times (N = 11, range 3–9 times).

During feeding, *D. missouriensis* sometimes flew to new perches. They removed the prey from their hypopharynx and carried them as described previously. Most flights were short (N = $62, \bar{x} = 4.0$ m, range 0.5–9.0), and were usually initiated by other insects, strong winds, or myself. Prey were invariably manipulated at the new perch before feeding resumed.

Over 77% of the prey (N = 197) were immobilized by inserting the hypopharynx into the dorsal regions of the victims, e.g., head, cervix, and thorax. Lavigne and Holland (1969) reported that *D. angustipennis*, whose diet is also predominantly Hymenoptera, behaves similarly by immobilizing its prey in these regions; and they suggested that it enables the asilid to avoid the prey's sting.

Diogmites missouriensis employed specific strategies to immobilize beetles, Anisodactylus sanctaecrucis Fab. and Neoclytus scutellaria (Oliver); pentatomids, Holcostethus limbolarius (Stål.) and Solubea pugnax (Fab.); and large flies, Diogmites missouriensis and D. platypterus Loew. Beetles and pentatomid prey were penetrated through the softer posterior end of the abdomens. This behavior was apparently in response to "hard" dorsal surfaces of these prey. When large dipterous prey (>17 mm) were attacked, the pair dropped into the vegetation where the asilids pinned their prey to the substrate and, subsequently, inserted the hypopharynx into their heads. Although feeding was sometimes completed at this location, prey were usually carried to a new location.

Specimens of *D. missouriensis* were observed feeding (N = 253) during most census periods, the earliest being at 0847 hrs and the latest at 1710 hrs (Fig. 1). However, over 83% of the feeding asilids were found between 1030 and 1500 hrs. The absence or limited feeding by *D. missouriensis* during early or late periods was influenced by at least three factors. One, higher rates of feeding occurred when prey were active and concentrated around flowering plants. Major prey items (bees, wasps, and flies) were most abundant on flowering plants between 1100 and 1430 hrs when a greater number of predators were observed feeding (Fig. 1). Two, environmental factors, such as heavy dew, influenced the onset of predation. On two mornings (6 and 7 August) when vegetation was "dripping" with water, neither foraging flights nor predators with prey were observed until after 1000 hrs when most of the vegetation had dried. This is in contrast to other days when dews were minimal or absent and vegetation was dry. Foraging flights were ob-

	Total Prey	% Diet	Prey Measured	Prey length (mm)	
Prey Orders				ž S.D.	Range
Hymenoptera	122	48.1	49	7.43 ± 2.61	4.1-12.70
Diptera	57	22.7	35	13.41 ± 3.71	6.0-18.75
Coleoptera	39	15.5	19	8.98 ± 2.25	5.6-10.60
Hemiptera	28	11.1	16	7.16 ± 1.35	5.0-8.70
Misc.	7	2.6	4	10.31 ± 4.09	6.8-15.00
	253	100.0	123	9.56 ± 3.90	4.1-18.75

Table 1. Dietary composition and body lengths of prey taken by *Diogmites missouriensis* in Jonesboro, Arkansas during August 1978.

 \bigcirc Predator (N = 25; $\bar{x} = 18.49 \pm 1.53$ S.D.)

 δ Predator (N = 25; $\bar{x} = 17.23 \pm 1.12$ S.D.)

served as early as 0815 hrs on these days. Presumably wet conditions delayed flight activities of major prey in the study area and resulted in delayed predatory activity by *D. missouriensis*. Three, in early morning (0700–0930 hrs) males flew slowly around and over the vegetation actively searching for females with which to mate. Searching behaviors and matings undoubtedly displaced predatory activities of males and interrupted that of females. Other studies (Dennis and Lavigne, 1976; Scarbrough and Norden, 1977; Scarbrough, 1978a, b; Hespenheide, 1978) have shown that predatory behaviors decrease as reproductive behaviors increase.

At the completion of feeding, most prey (N = 142) were dropped when D. missouriensis was in the act of manipulation. A few prey (N = 36) were dropped in flight as the asilids moved to new locations, foraged, or when they were disturbed. Also, some prey (N = 19) were pushed off the asilid's hypopharynx with the fore tarsi at the feeding site. The latter is the usual method by which several asilid species remove prey (Lavigne and Holland, 1969; Dennis and Lavigne, 1975).

PREY

Table 1 shows the dietary composition and body lengths of prey by orders taken from feeding *D. missouriensis* during this study. Hymenoptera formed the major prey category with Diptera, Coleoptera, and Hemiptera following in order of importance. The results also show a limited prey selection within each of the four major insect orders, with as few as nine genera taken from Hymenoptera, nine from Diptera, five from Coleoptera, and four from Hemiptera. These results agree with the general statement that most *Diogmites* spp. (Bromley, 1936) feed primarily on aculeate Hymenoptera. *Diogmites misellus* feeds on small Hymenoptera and Diptera (Bromley, 1946) and sometimes takes honey bees (Bromley, 1936). More recently, *D. angustipennis* (Lavigne and Holland, 1969) has been shown to take prey from



Fig. 2. Prey of Diogmites missouriensis arranged according to size classes (mm).

a limited number of insect orders but selected primarily aculeate Hymenoptera.

The mean size of prey taken by *D. missouriensis* was 9.56 mm and ranged from 4.1 to 18.75 mm (Table 1). However, an analysis of variance showed that mean prey body lengths of the four important orders were significantly different (P < .01) with Diptera being the largest prey taken (Scheffe' F-Test; P < .01). No significant difference in mean body lengths was found between other comparisons of prey orders.

The mean predator to prey size for *D. missouriensis* is 2.04. This indicates that the asilids were over two times larger than their prey. Females are larger (two-way analysis of variance; F = 7.07, P < .05) than males and catch larger prey (N = 88, $\bar{x} = 9.88 \pm 3.51$ mm; F = 10.38, P < .05) than do males (N = 35, $\bar{x} = 7.6 \pm 4.26$ mm). Females thus have a smaller mean predator to prey size ratio than do males, 1.87 and 2.27, respectively.

Figure 2 shows prey of *D. missouriensis* arranged according to size classes. Over 90% of the prey were 14 mm or less in length with larger prey items consisting of asilids, tachinids, tiphiid wasps, acridid grasshoppers, and staphylinid beetles. Males selected a disproportionately larger sample of prey (77.7% of diet) in size classes 4.1 to 8.0 mm than females (31.8% of diet). Eighty-four percent of the prey captured by females fell within size classes 6.1 to 14.0 mm. A small proportion of the prey captured by males fell within the larger sizes, indicating that they are capable of capturing

	Sex of Predator	
Prey Taxa	Female	Male
COLEOPTERA		
Carabidae: Selenophorus near planipennis LeC. Anisodactylus sanctaectucis Fabr. Cerambycidae: Neoclytus scutellaria (Oliver) Cleridae: Phyllobaenus sp.	4 20 1 1	2 4 —
Scarabaeidae: Onthophagus hecate hecate (Panzer) Staphylinidae: Unidentified	6 1	_
DIPTERA		
Unidentified Asilidae: Diogmites missouriensis Bromley D. platypterus Loew Psilocurus birdi birdi Hull Callophoridae: Unidentified Syrphidae: Palpada vinetorum (Fabr.) Toxomerus marginatus (Say) Tabanidae: Silvius sp. Tachinidae: Archytas apicifer (Walker) Unidentified	4 7 4 1 13 1 12	$\frac{-2}{1}$ 1 $\frac{-3}{2}$
EPHEMEROPTERA	1	
Neoephemeridae: Unidentified	1	_
HEMIPTERA		
Corizidae: Unidentified Lygaeidae: Eremocoris sp. Unidentified Pentatomidae: Solubea pugnax (Fabr.) Holcostethus limbolarius (Stål.)	1 1 4 5 10	 1 5
HOMOPTERA		
Membracidae: Thelia sp.	_	2
HYMENOPTERA		
Apidae: Apis mellifera L. Braconidae: Unidentified Chrysididae: Holopyga ventralis (Say) Formicidae: Fornica sp. Halictidae: Dialictus versatus (Robertson) Pompilidae: Anoplius illinoensis (Robertson) Priocnemis cornica Say Sphecidae: Astate sp.	15 3 6 3 8 13 2 1	3 38 4 6
Tiphiidae: <i>Tiphia</i> sp. <i>T. popilliavora</i> Rohwer	8 7	3 1

Table 2. Prey of *Diogmites missouriensis* arranged according to sex of the predator. All prey were collected or observed in the 22-acre plot in south Jonesboro, Arkansas, between July 2 and August 8, 1978. In some instances specific identification was not possible due to the poor condition of the prey, or the prey was not collected.

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Table 2. Continued.

	Sex of Predator	
Prey Taxa	Female	Male
NEUROPTERA		
Chrysopidae: Chrysopa sp.	1	-
ORTHOPTERA		
Acrididae: Unidentified nymphs	3	—

some large prey when the opportunity exists. An analysis of prey orders showed that hymenopterous prey taken by males were significantly smaller (N = 27, $\bar{x} = 5.79 \pm 1.50$ mm; F = 6.57, P < .001) than those taken by females (N = 27, $\bar{x} = 7.86 \pm 2.65$ mm). Furthermore, males captured mostly halictid bees, whereas females captured a wider range of hymenopterous and other prey types (Table 2). No significant differences were found between sizes of the remaining prey orders captured by the two sexes.

Why do females select a wider range of prey than males? Field observations showed that males and females fed at the same times during the day. Thus, prey taken by females were equally available to males. Females probably have significantly greater metabolic requirements than do males due to a larger body and the continuous production of eggs. Females then can less afford to specialize on specific prey taxa or on prey whose bodies can contribute a limited amount of energy.

Like other asilids (Lavigne and Holland, 1969; Dennis and Lavigne, 1975), D. missouriensis became prey for other predaceous arthropods and sometimes for members of its own species, e.g., cannabalism. Diogmites missouriensis fell victim to Phidippus clarus Keyserling (Araneida: Saltricidae), D. platypterus (Diptera: Asilidae), and D. missouriensis, 1, 6, and 10 times, respectively.

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